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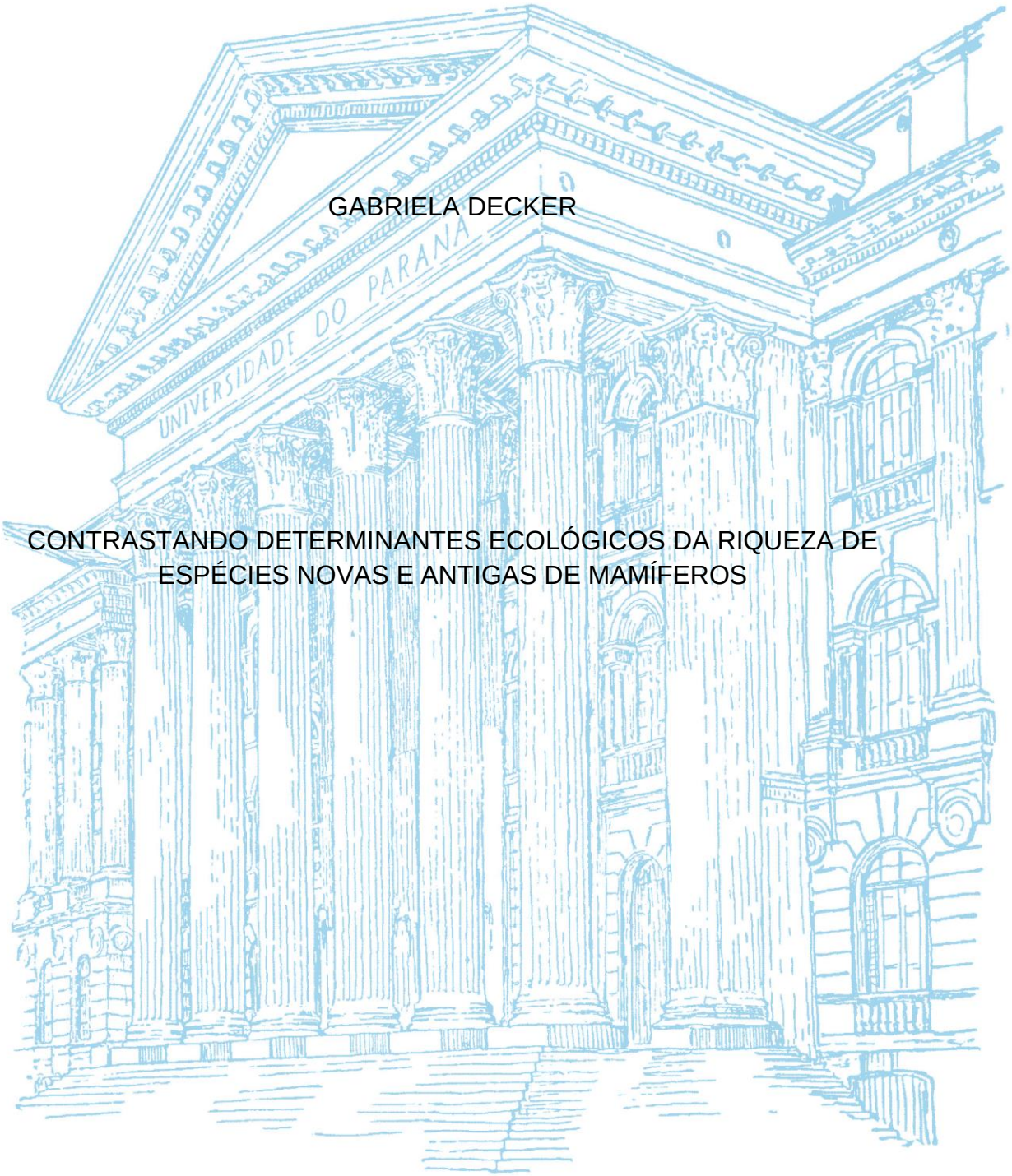

GABRIELA DECKER

CONTRASTANDO DETERMINANTES ECOLÓGICOS DA RIQUEZA DE ESPÉCIES NOVAS E ANTIGAS DE MAMÍFEROS

CURITIBA

2015

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CONTRASTANDO DETERMINANTES ECOLÓGICOS DA RIQUEZA DE ESPÉCIES NOVAS E ANTIGAS DE MAMÍFEROS

Dissertação apresentada como requisito parcial à obtenção do grau de Mestre em Ecologia e Conservação, no Curso de Pós Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná.

Orientador: Marcio R. Pie

CURITIBA

2015

Ministério da Educação
UNIVERSIDADE FEDERAL DO PARANÁ
Setor de Ciências Biológicas
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ECOLOGIA E CONSERVAÇÃO

PARECER

Os abaixo-assinados, membros da banca examinadora da defesa da dissertação de mestrado, a que se submeteu **Gabriela Decker** para fins de adquirir o título de Mestre em Ecologia e Conservação, são de parecer favorável à **APROVAÇÃO** do trabalho de conclusão da candidata.

Secretaria do Programa de Pós-Graduação em Ecologia e Conservação.

Curitiba, 20 de março de 2015.

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There is a pleasure in the pathless woods,
There is a rapture on the lonely shore,
There is society, where none intrudes,
By the deep sea, and music in its roar:
I love not man the less, but Nature more.
G.G. Byron

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RESUMO

Os gradientes de diversidade de espécies possivelmente estão entre os fenômenos mais comuns e menos conhecidos da ecologia. Os padrões espaciais de diversidade são resultado da interação de processos ecológicos e evolutivos. Em particular, a hipótese de conservação tropical de nicho é uma abordagem que explica com a conservação de nicho pode explicar os gradientes de riqueza de espécies face das mudanças climáticas ao longo do tempo evolutivo. A hipótese é baseada nas premissas de que climas mais quentes foram mais difundidos no passado e de que muitos grupos de espécies se originam em condições tropicais e tiveram dificuldade em entrar em novas condições de clima temperado, devido à conservação de suas características ecológicas. Comumente, esta hipótese é testada por testes que correlacionam características ambientais e filogenéticas, tais como a idade dos clados. Por exemplo, comunidades temperadas e regiões desérticas menos diversas tendem a conter mais espécies de clados derivados, enquanto as áreas tropicais quentes e úmidas suportam espécies de clados mais basais. Isto reflete a incapacidade de muitos clados que inicialmente evoluíram sob condições mais úmidas e quentes, em se adaptar às mudanças climáticas em escalas continentais, tendo assim, sobrevivido em áreas onde a alta precipitação e vegetação abundante persistiram. Neste estudo, nós testamos esses cenários utilizando dados da idade das espécies (inferida pelo respectivo tempo divergência do ancestral comum mais recente) para avaliar as diferenças entre correlatos ecológicos de riqueza de espécies novas e espécies antigas. O estudo incluiu cinco clados de mamíferos terrestres - Marsupiais, Primata, Chiroptera, Artiodactyla, e Carninora. Espécies que divergiram antes ou depois de 10 Mya de seu ancestral comum mais recente foram categorizadas como novas ou antigas, respectivamente. Este idade divide períodos com histórias climáticas notavelmente distintas. Neste estudo, nós verificamos que as diferenças nos correlatos ecológicas das espécies de novas e antigas de mamíferos são altamente dependentes da escala taxonômica, sugerindo que o grau de conservação de nicho é variável entre os clados. Desta forma, as idiossincrasias dos clados são relevantes, ressaltando que é preciso ter precaução em fazer previsões gerais a partir de conclusões alcançadas para grupos mais específicos. O nosso estudo desafia a visão tradicional de que a conservação de nicho é um fator fundamental na estruturação dos padrões de riqueza de espécies.

Palavras-chave: riqueza de espécies, correlatos ecológicos, idade das espécies, conservação de nicho.

ABSTRACT

Geographical patterns of diversity and the uneven distribution of species over space are possibly the most ubiquitous and the least understood phenomena in ecology. Recently, the tropical niche conservatism hypothesis has been invoked to explain latitudinal diversity patterns the tropical niche conservatism. This integrative approach outlines how niche conservatism explains contemporary species richness gradients in the face of climate change over evolutionary time. This hypothesis is based on the premises that warmer climates were more widespread in the past, many extant groups originated in tropical conditions and species experienced difficulty to break into new temperate-zone conditions due to conservatism in their ecological requirements. A common test of tropical niche conservatism hypothesis is to examine correlations between environmental and phylogenetic characteristics such as average taxon age. For instance, less diverse temperate communities and desert regions tend to contain more species from derived clades, while warm and wet tropical areas support species from more basal clades, reflecting the inability of many clades that initially evolved under wetter and warmer conditions to adapt to continental-scale climate change, having survived in areas where high precipitation and abundant vegetation persisted. In this study, we tested those scenarios using neontological data to assess differences in ecological predictors of species richness in old versus new species. We include five large terrestrial mammal clades in the analyses - Marsupialia, Primates, Chiroptera, Artiodactyla, and Carnivora – with each species being categorized as either old or new relative to its time for the most recent common ancestor (TMRCA) being above or below 10 Mya, an age that divides periods of markedly different climatic histories. In this study, we found that the differences in ecological correlates of old and new mammal species are highly dependent on the taxonomic scale suggesting that the degree of niche conservatism is variable among distinguished mammal clades. Therefore, idiosyncrasies of clades are important and care must be taken in making more general conclusions from results reached for a specific group. Our study challenges the traditional view that niche conservatism is the main driver underlying the ubiquitous climate-richness pattern.

Keywords: species richness, ecological correlates, species ages, niche conservatism.

SUMÁRIO

INTRODUÇÃO GERAL

Uma das principais motivações da ciência naturais é a busca por padrões. Entretanto, a complexidade dos fenômenos naturais torna generalizações em Ecologia mais difíceis do que nas ciências exatas. Ainda assim, diversos padrões são observados na natureza e se os padrões se repetem, possivelmente eles compartilham os mecanismos que os geraram. Um destes padrões biológicos é observado na distribuição geográfica da riqueza de espécies. As regiões tropicais abrigam uma riqueza de espécies desproporcionalmente maior do que as regiões temperadas, gerando um padrão espacial amplamente conhecido como “gradiente latitudinal de diversidade”. O gradiente latitudinal de diversidade, reconhecido na literatura como “maior padrão inexplicado da história natural” (Ricklefs 1989) e “padrão ecológico mais antigo” (Hawkins 2001), foi identificado no mundo natural quase um século antes da Ecologia ter se solidificado como ciência.

O gradiente latitudinal de diversidade é onipresente em organismos de água doce (France 1992, Stomp 2011), marinhos (Rombouts et al. 2009, Barton et al. 2010) e de ambientes terrestres (McCoy & Connor 1980, Soria-Carrasco & Castresana 2012), incluindo desde organimos procariotos (Fuhrman et al. 2008), invertebrados (France 1992, Rombouts et al. 2009), vertebrados (McCoy & Connor 1980) e plantas (Silvertown 1985). Uma metanalise recente (Hillebrand 2004) que avaliou quase 600 estudos, demonstrou que o padrão é consistente ao longo do espaço, escala, habitat e classificação taxonômica. Apesar dos esforços exercidos pelos ecólogos e biogeógrafos ao longo de mais de 200 anos de estudos, ainda não existe uma hipótese que seja universalmente aceita para explicar os mecanismos envolvidos na geração e manutenção no padrão atual de diversidade. Ainda assim, a tentativa em explicar o gradiente latitudinal diversidade continua sendo um dos grandes desafios contemporâneos da biogeografia e macroecologia (Willig et al. 2003).

Os naturalistas que participaram das expedições no séculos XVIII e IX foram os primeiros a perceber as variações existentes na distribuição global da riqueza de espécies. Alexander Von Humbolt foi o primeiro a documentar o

padrão na literatura. Em seu livro publicado em alemão Ansichten der Natur (1808), escrito após viagens pela Europa e América do Sul, Von Humbolt descreve a exuberância e ampla variedade de formas e cores dos ecossistemas tropicais e a maneira na qual as formas de vida diferem em ambientes com diferentes temperaturas. Apesar de não usar o termo atual biodiversidade ou riqueza, Von Humbolt fez previsões claras sobre como mecanismos climáticos estariam relacionados com as variações de formas nos ambientes tropicais e temperados. O mais interessante é que muitas hipóteses atuais contém em suas premissas mecanismos já sugeridos pelo naturalista a mais de 200 anos (Hawkins 2001).

O gradiente de riqueza foi também reconhecido claramente pelos progenitores da Teoria Evolutiva (Wallace 1878, Darwin 1862) e foi explorado por diversos ecólogos influentes do século passado (Dobzhansky 1950, Hutchinson 1959, MacArthur 1972). Particularmente, Dobzhansky (1950) integrou ideias com enfoque evolutivo para tentar explicar a geração dos padrões latitudinais. Entretanto, devido à indisponibilidade de dados e a limitações teóricas, as hipóteses com contexto evolutivo só puderam ser exploradas na literatura após algumas décadas. Pianka (1966) foi o primeiro a sintetizar as ideias propostas até a metade da década de 60. As primeiras hipóteses abordavam principalmente diferenças bióticas e ecológicas entre as regiões temperadas e tropicais para tentar explicar o padrão (e.g Kopfler 1959, Connel & Orias 1964, Willians 1964, Paine 1966). Neste período, a desvantagem da insuficiência de dados ecológicos limitava os ecólogos à teorização e especulação, gerando hipóteses variadas, porém, com problemas metodológicos para serem testadas ou falseadas. Durante as décadas de 70 e 80 as hipóteses antigas foram exploradas e aprimoradas e inúmeras novas hipóteses foram propostas (e.g Janzen 1970, Boucot 1975, Rathke & Price 1976, Sale 1977, Strong 1977, Huston 1979, McCoy & Connor 1980, Thiery 1982, Brown & Gibson 1983, Begon et al. 1986, Rohde 1989) . Apesar do aumento no número de hipóteses alternativas disponíveis na literatura, muitas delas eram circulares e interligadas e o estabelecimento de predições gerais era limitado à carência de dados. Ainda existia a necessidade de um menor número de hipóteses e que estas fossem mais testáveis.

O advento da Macroecologia nos anos 90 foi fundamental para superar muitas das limitações metodológicas e primordial para os avanços no estudo do tema (Brown & Maurer 1989, Brown 1995, Gaston & Blackburn 2000). A maior disponibilidade de dados ecológicos de distribuição das espécies, dados evolutivos no formato de filogenias mais robustas e completas e informações ambientais (e.g clima, vegetação) em ampla escala geográfica bem como o aumento da capacidade computacional para processar e analisar esses dados, reascendaram o interesse dos ecólogos pelos padrões em grandes escalas (Diniz-Filho et al. 2009). Atualmente, fatores climáticos, geográficos e históricos são amplamente abordados na literatura, e mais recentemente dados de registros fósseis tem auxiliado no desenvolvimento dos estudos.

As hipóteses ecológicas associam diretamente fatores relacionados ao ambiente (e.g precipitação, produtividade, temperatura, disponibilidade de energia) a riqueza de espécies. Elas foram propostas e discutidas desde o princípio dos estudos (Pianka 1966) e continuaram a ganhar força na literatura devido aos suportes empíricos e principalmente a estudos meta-analíticos que as reforçam (e.g Hawkins et al. 2003a). Dentre os mecanismos ecológicos, aqueles relacionados as condições climáticas e disponibilidade de energia são os mais discutidos e para os quais existem mais resultados que os suportam (e.g Currie 1991). Apesar de existir um sucesso relativo na descrição dos gradientes latitudinais de riqueza em relação às condições ambientais como temperatura e produtividade, há uma série de problemas em ligar diretamente as variações na riqueza a componentes ecológicos, principalmente porque as explicações com base na produtividade dos ecossistemas (Hawkins et al. 2003b) explicariam melhor as variações na abundância e não diretamente as variações na riqueza (Diniz-Filho et al. 2009).

Os efeitos históricos e evolutivos devem ser consideravelmente importantes para explicar os mecanismos associados a esses gradientes, e o desenvolvimento de uma teoria robusta para explicar os gradientes latitudinais de riqueza deve abordar de forma explícita processos macroevolutivos como especiação e extinção (Cracraft 1985, Rosenzweig 1995, Gaston & Blackburn 1996). A literatura foi renovada nas últimas décadas através de explicações históricas e evolutivas devido ao aumento na disponibilidade de dados filogenéticos, paleontológicos e biogeográficos (Currie et al. 2004). Ao contrário

dos modelos puramente ecológicos, as abordagens evolutivas que tentam explicar a gradiente latitudinal de diversidade têm focado em mecanismos relacionados a variações nas taxas de diversificação e no tempo disponível para especiação entre as regiões tropicais e temperadas (Mittelbach et al. 2007, Brown 2014).

Pelas hipóteses baseadas nas taxas de diversificação, a maior diversidade nas regiões tropicais seria causada por uma maior taxa de diversificação, mas esta poderia ser obtida por diferentes combinações de padrões geográficos nas taxas de extinção e especiação (revisado em Mannion et al. 2013). A hipótese de trópicos como museus ou berçários é uma abordagem evolutiva que prevê como a combinação dos mecanismos de especiação e extinção poderia gerar as diferenças na riqueza de espécies em ambientes temperados e tropicais. Os trópicos seriam considerados berçários evolutivos caso fossem responsáveis por gerar novos tipos de organização que enviando migrantes para colonizar o mundo extratropical. Por outro lado, os trópicos como museus serviriam como santuários para idades evolutivas antigas onde os organismos que eram amplamente distribuídos no passado geológico sobreviveram como relíquias. Esta hipótese prevê que espécies novas e antigas apresentariam gradientes latitudinais distintos. Gradientes dominados por espécies novas seriam evidências do modelo de diversificação de trópicos enquanto que gradientes dominados por espécies antigas evidenciariam o modelo de trópicos como museus.

A hipótese de tempo evolutivo (Fisher 1960) foi uma das primeiras hipóteses a incorporar efeitos históricos como mecanismo atuante na geração dos padrões de riqueza. Ela sugere que os ambientes tropicais tiveram uma história evolutiva mais longa e relativamente com poucos distúrbios quando comparadas as regiões temperadas, desta forma, são mais ricos, pois forneceram mais tempo para as linhagens acumularem espécies. Ela é suportada por evidências fósseis (Crane & Lidgard 1989, Jablonski 1993, Jablonski et al. 2006) e filogenéticas (Stephens & Wiens 2003) de clados que se originaram e acumularam suas linhagens nos trópicos. A hipótese de conservação tropical de nicho (TNC) (Latham & Ricklefs 1993, Wiens & Donoghue 2004), é uma extensão da hipótese de tempo evolutivo que incorpora fatores históricos, evolutivos e ecológicos. Wiens e Donogue (2004)

uniram os conceitos evolutivos da conservação filogenética de nicho e limitações na dispersão das espécies com a história dos trópicos para formular uma proposta abrangente na tentativa de explicar a geração da ampla diversidade tropical. A TNC assume que os clados se originaram nos trópicos (porque os trópicos são mais antigos e cobrem áreas maiores) e as transições das linhagens dos trópicos para zonas temperadas são raras, pois as espécies conservam o nicho climático dos seus ancestrais, limitando assim, a dispersão das linhagens para ambientes mais frios (Latham & Ricklefs 1993, Wiens & Donoghue 2004, Wiens et al. 2006). Uma das previsões da TNC é que a idade dos táxons deve diminuir com o aumento da latitude, sendo que a riqueza dos trópicos seria então dominada por espécies antigas enquanto que as regiões temperadas abrigariam principalmente espécies evolutivamente mais recentes.

Uma das formas de investigar as previsões da TNC é através do uso de análises estatísticas que investiguem a relação entre o clima e a riqueza de táxons com diferentes idades. Buckley et al. (2010) encontrou que, em mamíferos, as correlações riqueza-clima positivas (mais espécies em temperaturas quentes) são formadas por clados antigos de origem tropical enquanto que clados mais recentes apresentam correlações clima-riqueza negativas (mais espécies em temperaturas frias), com a idade dos clados coincidindo com a expansão das zonas temperadas durante o Eoceno tardio. Outro estudo recente (Romdal et al. 2013) investigou uma variedade de grupos de organismos, aquáticos e terrestres, e encontrou que relações riqueza-latitude são relacionadas pela temperatura nas quais os grupos se originaram. Estes resultados podem indicar que diferentes condições climáticas podem estar estruturando os gradientes de riqueza de espécies novas e antigas, bem como evidenciar a conservação de nicho climático como um mecanismo evolutivo fundamental para formação dos padrões atuais de riqueza.

Abordagens que incorporam a história evolutiva das espécies através de estimativas de suas idades constituem, portanto, importantes ferramentas para elucidação de mecanismos históricos envolvidos na estruturação dos padrões atuais de riqueza. Porém, muitas filogenias disponíveis são incompletas, e testes empíricos das previsões da TNC disponíveis na literatura têm se limitado a utilizar a idade de origem de famílias (Buckley et al. 2010), a idade de grupos polifiléticos como macroalgas, macroinvertebrados, plantas e vertebrados

(Romdal et al. 2013), ou ainda métrica de desenvolvimento evolutivo que mensura a medida da distância de raiz (uma métrica que quantifica o número de nós que separam o táxon terminal da raiz da árvore (Kerr & Currie 1999), mas que pode ser problemática pois não contém nenhuma informação direta da idade das espécies. Entretanto, as adaptações biológicas ocorrem ao longo de tempo de duração das espécies e as espécies são formadas em escalas de tempo mais recentes do que a dos grandes clados investigados na literatura. Diante do exposto, a proposta deste trabalho é investigar mecanismos que possam estar atuando na geração dos padrões de riqueza de espécies novas e antigas em uma abordagem que investiga a escala de tempo típica de formação destas espécies. Mais especificamente, nós investigamos uma das previsões da hipótese de TNC de que as condição ecológicas relacionada ao padrão de riqueza atual das espécies deve refletir as condições climáticas presentes no período no qual as espécies foram formadas.

REFERÊNCIAS

Barton, A.D., Dutkiewicz, S., Flierl, G., Bragg, J., Follows, M.J. 2010. Patterns of Diversity in Marine Phytoplankton. Science 327: 1509-1511.

Begon, M., Harper, J. L. and Townsend, C. R. 1986. Ecology. Individuals, populations and communities. Blackwell, Oxford

Boucot, A. J. 1975. Evolution and extinction rate controls. Elsevier, Amsterdam

Brown, J. H. & Gibson, A. C. 1983. Biogeography. Mosby, St. Louis.

Brown, J. H. & Maurer B. A. 1989. Macroecology: the division of food and space among species and continents. Science 243: 1145-1150.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago

Brown, J. H. 2014. Why are there so many species in the tropics? J. Biogeogr. 41: 8-22.

Connell, J. H. & Orias, E. 1964. The ecological regulation of species diversity. Am. Nat. 98: 399-414

Cracraft, J. 1985. Biological diversification and its causes. Ann. Missouri Bot. Gard. 72:794-822.

Crane, P.R. & Lidgard, S. 1989. Angiosperm diversication and paleolatitudinal gradients in Cretaceous oristic diversity. Science, 246: 675–678.

Currie, D. J. 1991. Energy and large-scale patterns of animal and plant-species richness. Am. Nat. 137: 27-49.

Currie, D.J. et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol Lett. 7: 1121–1134.

Darwin, C.R. 1859. The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London, UK.

Diniz-Filho, J. A. F. et al. 2009. Padrões e processos ecológicos e evolutivos em escala regional. Megadiversidade. 5: 5-16.

Dobzhansky, T. 1950. Evolution in the tropics. Am. Sci. 38: 208-221

Fisher, A. G. 1960. Latitudinal variations in organic diversity. Evolution 14: 64-81.

France, R. 1992. The North American Latitudinal Gradient in Species Richness and Geographical Range of Freshwater Crayfish and Amphipods. Am. Nat. 139: 342-354.

Gaston, K. J. & Blackburn, T. M. 1996. The Tropics as a Museum of Biological Diversity: An Analysis of the New World Avifauna. Proc. R. Soc. Lond. B 263: 63

Gaston, K. J. & Blackburn, T. M. 2000. Pattern and Process in Macroecology. Blackwell Science, Oxford

Hawkins, B. A. 2001. Ecology's oldest pattern? Trends Ecol. Evol. 16

Hawkins, B. A. et al. 2003a. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84: 3105-3117.

Hawkins, B. A., Porter, E.E. & Diniz-Filho, J. A. F. 2003b. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84: 1608-1623.

Hawkins, B. A.,. Diniz-Filho, J. A. F & Weis, A. E. 2005. The mid-domain effect and diversity gradients: is there anything to learn. Am. Nat. 166:E140-E143.

Hawkins, B.A. et al. 2006. Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of new World birds. J. Biogeogr. 33, 770–780

Hawkins, B.A. et al. 2007. Climate, niche conservatism, and the global bird diversity gradient. Am. Nat. 170, 16–27

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. Am. Nat., 163, 192–211.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113: 81-101.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104: 501-528

Jablonski, D. 1993. The tropics as a source of evolutionary novelty through geological time. Nature, 364, 142–144.

Jablonski, D., K. Roy, & Valentine, J. W. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science 314:102–106.

Latham, R. E. & Ricklefs, R. E. 1993b. Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. Oikos 67: 325-333.

Mannion, P. D. et al. 2013.The latitudinal biodiversity gradient through deep time. TREE-1756.

McCoy, E. D. & Connor, E. F. 1980. Latitudinal gradients in the species diversity of North American mammals. Evolution 34: 193-203.

Mittelbach, G. G. et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10, 315–331

Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65-75.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100: 33-46.

Rathke, B. J. & Price, P. W. 1976. Anomalous diversity of tropical ichneumonid parasitoids: a predation hypothesis. Am. Nat. 110: 889-893.

Ricklefs, R. E. 1989. The integration of local and regional processes. In Speciation and Its Consequences (ed. D. Otte & J. A. Endler), pp. 599–622. Sunderland, MA: Sinauer Associates.

Rohde, K. 1989. Simple ecological systems, simple solutions to complex problems? Evol. Theor. 8: 305-350

Rombouts, I. et al. 2009. Global latitudinal variations in marine copepod diversity and environmental factors. Proc. R. Soc. B 276: 3053-3062.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge: Cambridge University Press.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111: 337-359

Silvertown, J. 1985. History of a latitudinal diversity gradient: woody plants in Europe 13,000-1000 years b.p. Journal of Biogeography 12: 519-525.

Slobodkin, L. B. & Sanders, H. L. 1969. On the contribution of environmental predictability to

Stomp, M. et al. 2011. Large-scale biodiversity patterns in freshwater phytoplankton. Ecology 92:2096–2107.

Strong, D. R. 1977. Epiphyte loads, tree falls, and perennial forest disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. J. Biogeogr. 7: 215-218

Thiery, R. G. 1982. Environmental instability and community diversity. Biol. Rev. 57: 671-710

Willians C. B. 1964. Patterns in balance of nature. Academic Press, New York and London.

Wallace, A.R. 1878. Tropical Nature and Other Essays. Macmillan, New York.

Wiens, J. J., & Donoghue, M. J. 2004. Historical biogeography, ecology, and species richness. TREE 19: 639–644

Willig, M. R., Kaufman, D. M. & Stevens, R. D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Ann. Rev. Ecol. Syst. 34: 273–309.

Wiens, J. J. et al. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: tree frogs unearth the roots of high tropical diversity. Am. Nat. 168, 579–596

Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians. Am. Nat. 170: S86–S106.

Romdal, T., Araújo, M. & Rahbek, C. 2013. Life on a tropical planet: niche conservatism and the global diversity gradient. Global Ecol Biogeogr. 22.

Buckley, L. et al. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. Proc. R. Soc. Lond. B 277: 2131–8.

Constrasting ecological correlates of richness for old and new mammals species

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1 INTRODUCTION

A major goal in ecological studies is the search for patterns. However, the complexity of natural phenomena often hampers generalizations in biological sciences. Still, many patterns are observed in nature, and if these patterns are found at different levels of biological organization, it is likely that similar mechanisms might underlie the generation of these patterns. One of the most ubiquitous ecological patterns in biological diversity is the drastic increase in the number of species from poles to the tropics. This taxonomic tendency referred to as latitudinal diversity gradient is likely the “major unexplained pattern of natural history” (R. E. Ricklefs quoted in Lewis 1989), and, in spite of being documented almost a century before Ecology was established as a field of science, the ecological and evolutionary mechanisms generating and maintaining the pattern remains unknown (Mittelbach et al. 2007).

Despite the efforts made by ecologists and biogeographers over more than 200 years of study, no hypothesis is still universally accepted to explain the mechanisms involved in the generation and maintenance of the current pattern of diversity. The attempt to explain the uneven distribution of species richness remains one of the major contemporary challenges of biogeography and macroecology (Rahbek & Graves 2001; Willig et al. 2003; Brown 2014). For an extended period, the study of the latitudinal diversity gradient has been dominated by an ecological point of view, which relies on the potential effect of biotic and abiotic factors on environmental carrying capacity and limiting species coexistence (Willig, Kaufman, & Stevens et al. 2003). Such factors are strongly correlated with taxonomic richness through measures of temperature, water availability and productivity (Francis & Currie 2003; Hawkins et al. 2003; Currie et al. 2004; Hawkins, Diniz-Filho, & Soeller 2005, Field et al. 2009). However, regardless of the high correlation between diversity and environmental variables, purely ecological explanations do not reveal how evolutionary dynamics of species might mediate the establishment and maintenance of diversity patterns (Chown & Gaston 2000; Gaston 2000; Jablonski, Roy, & Valentine 2006; Mittelbach 2007). Therefore, linking

ecological and evolutionary processes is a necessary step to generate a full understanding of richness gradients (Ricklefs 2004).

Contrastingly, evolutionary explanations to the latitudinal diversity gradient have focused on mechanisms raised to explain the distribution of species based on the variation in rates of diversification and the amount of time available for speciation within regions (Mittelbach et al. 2007). Niche conservatism mechanism, defined as the tendency of species to retain niche-related ecological characteristics over time as the clade diversifies, is also raised in the attempt to explain diversity gradients (but see Pearman et al. 2008 and Losos 2008). Niche conservatism will determine the environmental conditions a species can tolerate and the regions it will be able to disperse into (Wiens & Graham 2005). The tropical niche conservatism, a more integrative hypothesis, outlines how niche conservatism can explain the contemporary species richness gradients in the face of climate change over evolutionary time. Briefly, the hypothesis was established based on the assumptions that most extant clades originated in warm and wet tropical conditions and that species experience difficulty to break into new temperate-zone conditions due to conservatism in their ecological requirements (Wiens & Donoghue 2004)

Studies investigating phylogenetic community structure supporting this idea has been evidenced in several studies on geographical gradients (e.g Wiens 2007; Hawkins, Diniz-Filho, & Soeller 2005; Hawkins et al. 2006) For instance, less diverse temperate communities and desert regions tend to contain more bird species from derived clades, while warm and wet tropical areas tend to support bird species from more basal clades (Hawkins, Diniz-Filho, & Soeller 2005; Hawkins et al. 2006). Comparisons of slopes of climate-richness relationship (Buckley et al. 2010) or latitude-richness relationship (Romdal et al. 2013), found that positive correlations are driven by older clades with tropical origins, whereas clades originating during cold periods presented shallower latitudinal species richness gradients. This pattern reflects the inability of many clades that initially evolved under wetter and warmer conditions to adapt to continental-scale climate change, having survived in areas where high precipitation and abundant vegetation persisted.

These findings might suggest that diversity gradients of new and old lineages might be driven by different underlying climatic conditions. Thereby, investigating species climatic niche attributes together with their evolutionary ages is likely to be valuable to explain large-scale biodiversity patterns. Yet, in the literature this tests are limited to investigate ages of origination entire clades and detailed investigation of species ages is still unexplored. Ecological adaptation occurs in the typical duration of single species and species are formed in more recent time scales than the major clades. Therefore, the aim of this proposal is to utilize a realistic estimation of species ages to explore the predictions of TNC. We investigate the environmental and climatic correlates associated to richness patterns of new and old species in five large mammal clades (Marsupialia, Chiroptera, Carnivora, Artiodactyla and Primates). We categorized species as either old or new if their time to most recent common ancestor was above or below 10 Mya, an age that divides periods of markedly different climatic histories. If niche conservatism is a main driver of species diversity patterns, we expect that current richness patterns of old and new species will reflect environmental conditions extant in evolutionary times in which species were generated, with warmer and wetter regions and closed forests being dominated by old species whereas new species would be more common in cooler, drier and open habitats.

2 MATERIALS AND METHODS

2.1 Phylogenetic analysis

Our analyses focused separately on five mammal clades, the infraclass Marsupialia, and the placental orders Chiroptera, Carnivora, Artiodactyla, and Primates. This level of taxonomic hierarchy was selected in order to avoid combining groups with highly distinct biogeographical histories (e.g. bats X marsupials). In spite of being the most representative mammalian order, Rodentia were excluded from the analysis given to uncertain geographical

distribuitons and phylogenetic relationships in species within the clade. The phylogenetic relationships of the studied taxa and their divergence times were obtained from the supertree of Bininda-Emonds et al. (2007). This phylogeny includes 4,510 of the 4,554 extant mammal species (according to Wilson & Reeder 1993) and is among the most comprehensive phylogenies available to date. Although some portions of the phylogeny include a level of resolution below 85% of the nodes, these regions are concentrated in the period around 50 Myr and therefore should not affect the results of our study. We are aware that there have been updates to the comprehensive phylogeny in the case of some taxa (e.g. Nyakatura & Bininda-Emonds 2012), yet we decided to base our analyses on the original phylogeny to ensure that all divergence times were estimated according to a single, coherent approach. The age of each species was inferred as the time since its most recent common ancestor. Species that diverged earlier or later than 10 Mya from their most recent common ancestor were categorized as old or new, respectively. Although this distinction is somewhat arbitrary, it was chosen given that it divides the datasets into roughly equal-sized partitions, and because it divides periods of markedly different climatic histories. Old species date from Paleocene to the middle Miocene a period characterized mainly by warm and wet conditions, with the period since 10 Mya to the present being characterized by a gradual cooling (see Zachos et al. 2001). Despite the climatic oscillations over the Cenozoic, old species arose in warmer and wetter conditions when compared to new species. The climatic cooling that happened over the Cenozoic was followed by an expansion of grasslands and contraction of closed forest habitats (Retallack 2000; Liu, Arens & Li 2007; Behresmeyer et al. 1992), an event that could strongly have led to the currently observed differences in richness of old and new species in relation to vegetation cover.

2.2 Species richness

The geographical information of the studied species was obtained in the form of shapefiles from de IUCN database (Version 2010.4). Digitized range maps of

mammal species were integrated into a grid containing cells of 110 km x 110 km to generate the species richness maps. We used the Cylindrical Equal Area projection to maintain a similar area in cell size over the entire globe. All the analyses were repeated separately to generate data of species richness for old and new species of each clade. We removed all aquatic species, non-native species and species with uncertainty in their places of occurrence. A total of 1547 species were included in the analysis (Table 1). We carried out the spatial analysis in ArcGIS 10.1 (ESRI 2011).

	Total	New species	Old species
All clades	1547	1073	474
Artiodactyla	151	114	37
Carnivora	198	141	57
Chiroptera	756	527	229
Marsupialia	236	130	106
Primates	206	161	45

Table 1. Number of species included in our analysis.

2.3 Environmental variables

We selected a set of environmental variables as potential correlates of species richness based on the path model proposed by Hawkins et. al (2012). This model is based on the assumption that the response of species richness to climate is mediated through its effect on plant biomass and through vegetation structure (Hawkins, Diniz-Filho, & Soeller 2005; Hawkins et al. 2006). In fact, the environmental variables included in the model have been shown as strong predictors of mammal and bird richness patterns (Hawkins et al. 2007, 2012). Environmental layers were obtained from online databases and included plant density (NDVI), mean annual temperature, actual evapotranspiration (AET), range in elevation, and an interaction between temperature and topography (T x Relev).

Normalized Difference Vegetation Index (NDVI) (available at *http://edit.csic.es/Soil-Vegetation-LandCover.html*) is an index of the density of plant growth obtained from satellite images. NDVI is computed by NDVI = (NIR - VIS)/(NIR + VIS), where NIR is the near infrared light and VIS is the visible red light reflected by a surface (Rouse et al. 1974). Plant green leaves highly reflect the near-infrared spectral region and absorb visible red spectral (Knipling 1970), resulting in positive NDVI values. NVDI values range from -1 to + 1, with low values of NDVI (0.1 and below) corresponding to deserts, rocky and snowy areas. Intermediate values represent shrub and grassland (0.2 to 0.3), high values indicate temperate and tropical rainforests (0.6 to 0.8), while water has negative NDVI values. The layer applied in this study had original NDVI real values (from -1 to +1) rescaled to a range from 1 to 255 (byte format). Available NDVI maps contain mean values for each month computed over an 18-year period (from 1982 to 2000, excluding 1994 data from calculation). We averaged monthly data to generate an annual average.

Mean annual temperature values were obtained from spatially interpolated climate data available in the WorldClim database *(http://www.worldclim.org/*). This dataset contains compiled monthly averages values from the 1950–2000 period at a 30 arc seconds resolution (Hijmans et al. 2005).

AET quantifies the amount of water removed from a surface through evaporation (due to radiation or temperature) and through plant transpiration (process of water movement through a plant and its evaporation through their leaves) (Willmott & Kenji 2001). Thus, it represents the simultaneous environmental water and energy availability (Stephenson 1990). AET is strongly related to plant productivity (Rosenzweig 1968), and has been shown as a strong predictor of global patterns of bird and mammal species richness (Hawkins et al. 2003a, Hawkins et al. 2012). Raster data comprises a time series of 50 years (from 1950 through 1999), and the grid points cover the globe at a 0.5x0.5 degree resolution (available at *http://www.sage.wisc.edu/atlas/data.php?incdataset=Evapotranspiration)*.

Range in elevation is a measure of the range between the minimum and the maximum elevation within each cell. Elevation range has been proposed to be a proxy of environmental heterogeneity (Hawkins et al. 2003). Habitats with

high heterogeneity support greater diversity by providing more available niche space (allowing more species to coexist) and opportunities for isolation and divergent adaptation (enhancing the probability of speciation events; reviewed in Stein et al. 2014). Elevation range values were obtained from the GTOPO30 digital elevation model (available at *http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/ gtopo30_ info*).

Finally, the last variable included in the model represents an interaction between temperature and range in elevation (T x Relev). Macroclimate interacts with topographic relief, generating mesoscale habitat gradients in warm tropical mountains. We obtained only positive temperature values by adding 21 to original temperature units in each cell. To generate the mesoscale interactions between topography and macroclimate, the transformed temperature values were multiplied by the range in elevation in each cell (as proposed by Hawkins et al. 2006, 2007).

2.4 Statistical analyses

We used path analysis based on Structural Equations Modelling (SEM) to investigate the relationships between current environment and mammal species richness. SEM is a statistical framework for simultaneously estimating complex relationships between variables. This technique offers a more reliable estimation approach than traditional methods such as simple multiple regressions analysis. SEM is referred to as a causal model because it represents hypothesized causal relationships among variables, and possibly revealing direct and indirect associations between predictor and response variables (Shipley 1997). We applied a path analysis derived from a model already shown to explain much of the variation of birds and mammals richness (Hawkins et al. 2007, 2012). This model investigates the direct and indirect effects of temperature in species richness through NDVI, AET and TxRelev. All variables were first standardized to a mean of zero and a variance of one to allow for the comparison of path coefficients connecting variables with different initial units. As we intend to investigate if new and old species gradients are

associated to distinct environmental gradients, we repeated the analysis separately for each age group.

The Infraclass Marsupialia is a diverse group that comprises seven orders, three occurring in American continent (Didelphimorphia, Microbiotheria and Paucituberculata) and four in Australasia (Dasyuromorphia, Notoryctemorphia, Diprodontia, Peramelemorphia; Aplin & Archer, 1987). Given that marsupials present a very uneven geographic distribution, and to account for the effects of biogeographic history, we also ran the analysis separately for marsupials of Australasia and New World. The path analysis were performed in the SEM library (Fox 2007) in R version 3.1 .1 (R Development Core Team 2013).

We controlled for the effects of spatial correlation in data through the eigenvector-based spatial filtering technique (SEVM, Griffith & Peres-Neto 2006). The eigenvectors were applied as spatial filters in partial regressions models designed to partition the variation in species richness explained by the environmental predictors, by geographical effects and by their overlap (as in Gouveia et al. 2014). For each clade, we used the environmental variable identified in the path analysis as the predictor having the strongest effect on species richness (AET, NDVI or TxRelev) as the environmental predictor in the partial regression analysis. The partial regression analysis partitions the variation in species richness into four components: (a) non-spatial environmental variation (local), (b) spatially structured environmental variation (regional), (c) spatial variation on species richness not shared by environmental variables and (d) variation not explained by the model (Borcard et al. 1992) Owing to computational limits, spatial analyses were calculated in random samples of 4000 cells. The spatial eigenvectors and the partial regression were performed using the SAM software (Rangel, Diniz-Filho & Bini 2010).

3 RESULTS

3.1 Ecological correlates of species richness

Dates of species origination ranged from < 1 to 65 million year ago (Ma), with most species originating closer to present (Fig. 1). When all clades are analyzed simultaneously, correlation patterns were very similar for old and new species (Fig. 2a, 3a-b). The path models identified AET as the environmental predictor having the strongest effect on richness for young and old species (r_{new} = 0.75 and r_{old} = 0.79). The measure of mesoscale climatic gradients (TxRelev) shows a moderate effect on richness patterns for both young and old mammals species (r_{old} = 0.21 and r_{new} = 0.23). Plant productivity measured by NDVI presented a weak negative effect (r_{old} = -0.08 and r_{new} = -0.01). The direct effect of temperature was also weak but positive for both old and young species (r_{old} = 0.17, r_{new} = 0.13). Conversely, the results of path models applied for each clade separately revealed highly distinctive and idiosyncratic patterns, with differences in the most important predictors and in the magnitude of standardized path coefficients for old and new species.

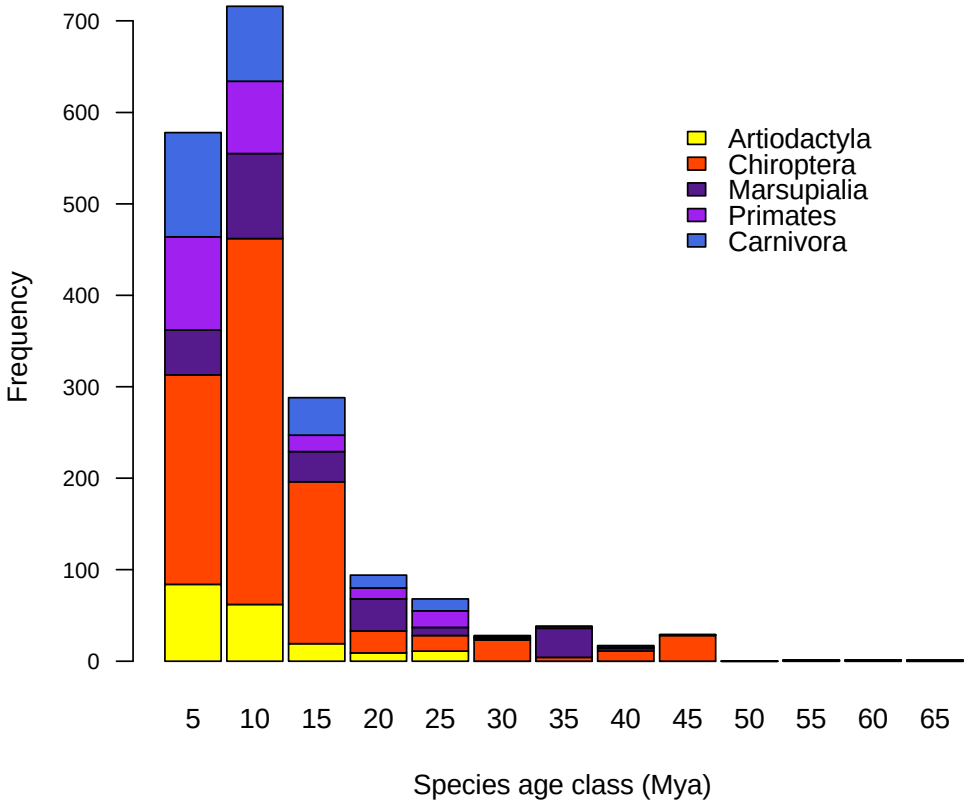

Fig. 1. Distribution of species ages of mammal clades included in the present study.

3.1.1 Artiodactyla

In general, the magnitude of most direct path coefficients for artiodactyls was lower when compared with the model for all clades (Fig. 2c-d, Fig. 3b). Richness of both old and new species of Artiodactyla is more affected by the mesoscale interaction between temperature and elevation (r_{old} = 0.38 and r_{new} = 0.38) than by AET. Water and energy availability had a weaker and similar effect for old and young species (r_{old} = 0.26 and r_{new} = 0.25). The direct effect of temperature was also weak, but old species are richer in warmer climates than new species (r_{old} = 0.23 and r_{new} = 0.11). NDVI had a negative effect on richness patterns of old species (*i.e.* more species in communities where plant productivity is lower) and no effect on richness of new species.

3.1.2 Carnivora

Evapotranspiration (r_{old} = 0.48 and r_{new} = 0.44) and environmental heterogeneity (r_{old} = 0.46 and r_{new} = 0.28) were predictors with the strongest effects on richness patterns of carnivores. As in artiodactyls, NDVI had a negative effect in old species, and no substantial effect in richness patterns of new species (r_{old} = -0.21 and r_{new} = 0.02). Old species of carnivores are also present in warmer regions, with richness of new species being negatively affect by temperature (r_{old} = 0.24 and r_{new} = -0.11) (Fig. 2e-f, Fig. 2c).

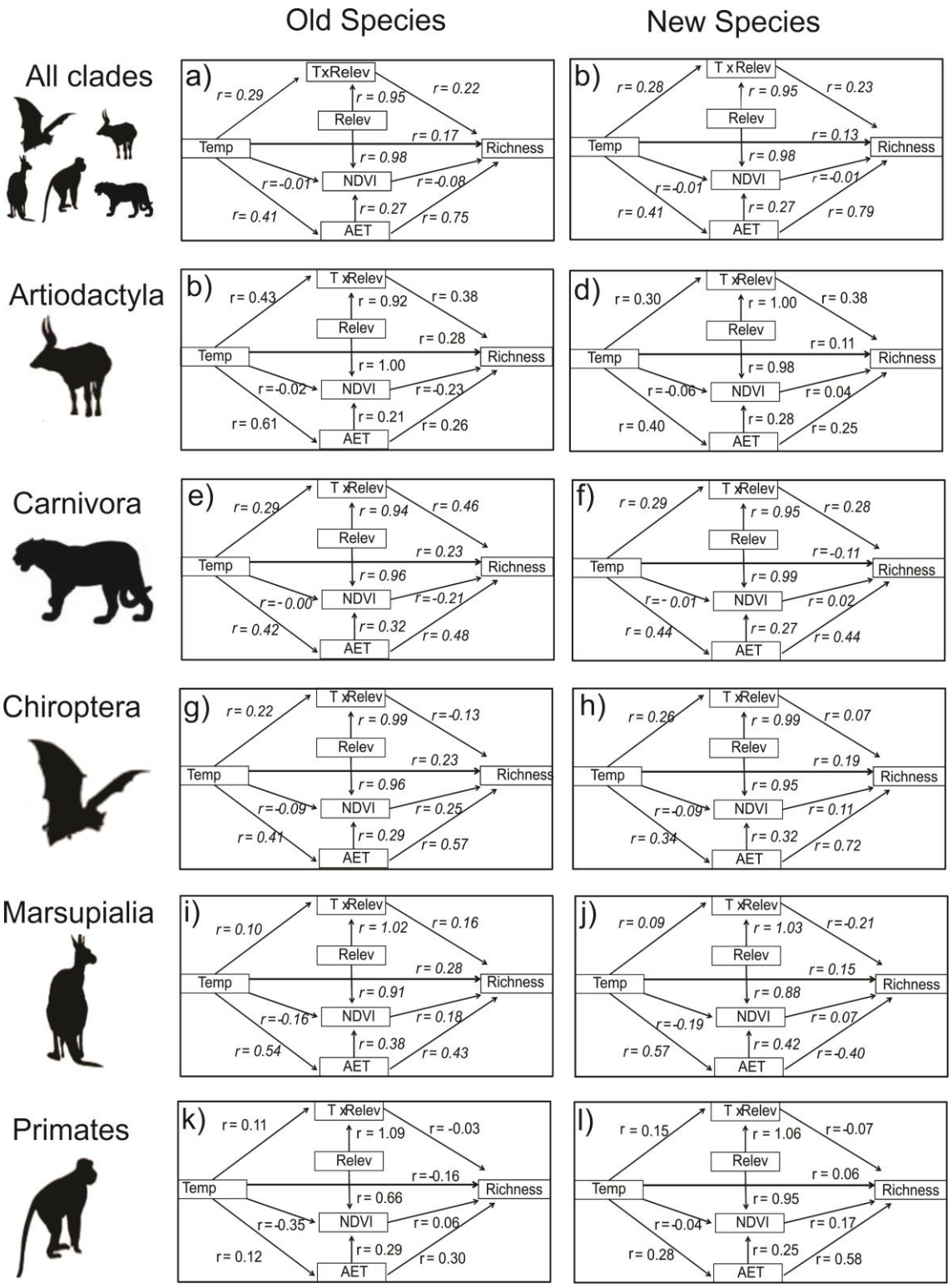

Fig. 2. Path models of the direct and indirect effect of temperature (Temp), evapotranspiration (AET), normalized differentiation index (NDVI) and the interaction between temperature and topography (TxRelev) on species richness of (a) new mammals, (b) old mammals, (c) old artiodactyls, (d) new artiodactyls, (e) old carnivores, (f) new carnivores, (g) old bats, (h) new bats, (i) old marsupials, (j) new marsupials, (k) old primates and (l) new primates.

3.1.3 Chiroptera

Path coefficients for bats are very similar to the results of the combined analysis for all clades, showing no marked differences between ecological correlates for old and new species (Fig. 2g-h, Fig. 3d). This result underscores the importance of bats (the richest clade) in shaping the global climatic-richness relationship of all mammals. Evapotranspiration was the environmental predictor having the strongest effect (r_{old} = 0.57 and r_{new} = 0.72), followed by temperature (r_{old} = 0.23 and r_{new}= 0.19), NDVI (r_{old} = 0.25 and r_{new}= 0.10) and TxRelev (r_{old} = 0.13 and r_{new}= 0.06) with increasingly smaller effects.

3.1.4 Marsupialia

Marsupialia showed the most dissimilar results between old and new species. (Fig. 2i-j, Fig. 3e). Evapotranspiration was the most important predictor of species richness, but influencing positively old species and negatively new species AET (r_{old} = 0.43 and r_{new}= -0.40). The interaction between climate and topography also showed opposite effects for old and new species (r_{old} = 0.16 and r_{new}=-0.20). The direct effect of temperature was stronger for old than for new species (r_{old} = 0.28 and r_{new}= 0.15), and NDVI showed a weak and positive effect for both (r_{old} = 0.18 and r_{new}= 0.07). In other words, old species of marsupials are richer in areas with higher availability of water and energy and in most heterogeneous communities, whereas new species of marsupials showed the opposite pattern The results of the analyses for Australasia and New Worlds evidenced distinct influence of ecological predictors in marsupial richness in the two continents (see supplemental material). Both, new and old Australasian marsupials had negative temperature coefficients (r_{old} = -0.26 and r_{new}= -0.13) and markedly differences on NDVI values (r_{old} = 0.42 and r_{new}= -0.08). Old and new American marsupials differed mainly in relation to AET (r_{old} = 0.58 and r_{new}= -0.39) and temperature coefficients (r_{old} = 0.07 and r_{new}= 0.45).

3.1.5 Primates

As in most clades, evapotranspiration was the most important predictor of species richness of primates, with positive effects for old and new species (r_{old} = 0.30 and r_{new}= 0.58). TxRelev had a weak negative effect, for both old and new species (r_{old} = -0.03 and r_{new} = -0.07). Plant productivity was also not important for old and new species (r_{old} = 0.06 and r_{new} = 0.18). Primates were the only clade that presented a negative correlation between temperature and richness of old species (r_{old} = -0.16), which was positive and weak for new species(r_{new} = 0.06).

3.2 Spatial structure of mammal species richness

The residuals of the relationships between mammal species richness and ecological correlates were strongly structured in space. A total of 14 and 6 eigenvectors from the SEVM were selected as spatial filters for old and new species, respectively. In old species (Fig. 4II), about 41% of variance on richness is explained solely by environmental variables, 57% of the explanation is shared between space and environmental correlates, with purely spatial structure being irrelevant, and accounting for 0.5% of the variation is species richness. For new species, about 24% of variance on richness is explained solely by environmental variables, 49% of the explanation is shared between space and environmental variables and solely space accounted only for 8% of the total variation (Fig. 4I).

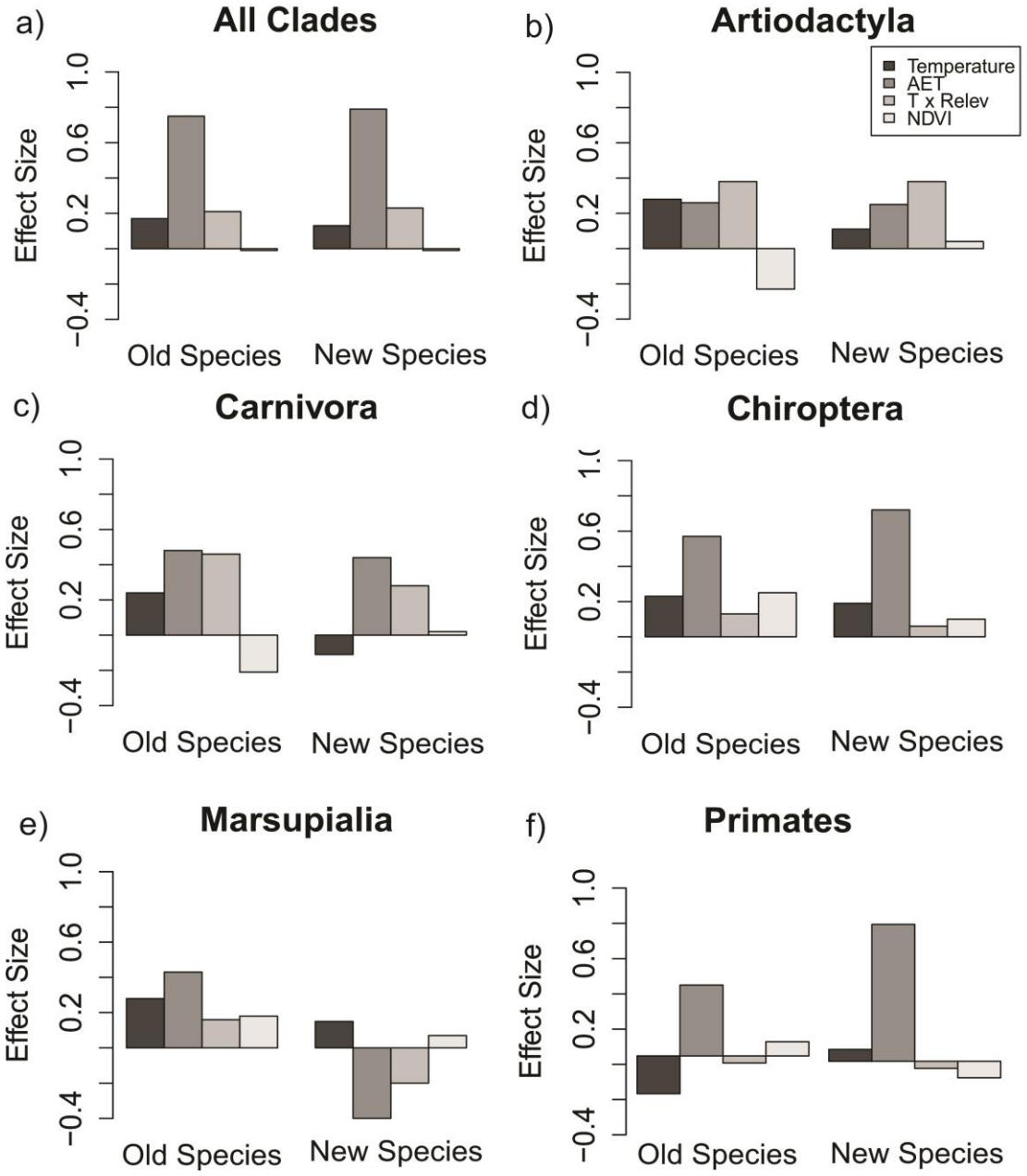

Fig. 3. Effect sizes of temperature, evapotranspiration (AET), environmental heterogeneity (TxRelev) and plant productivity (NDVI) on species richness of old and new species of all mammal clades (a) and for individual clades (b-f). Values represent standardized coefficients of direct paths of the path analysis.

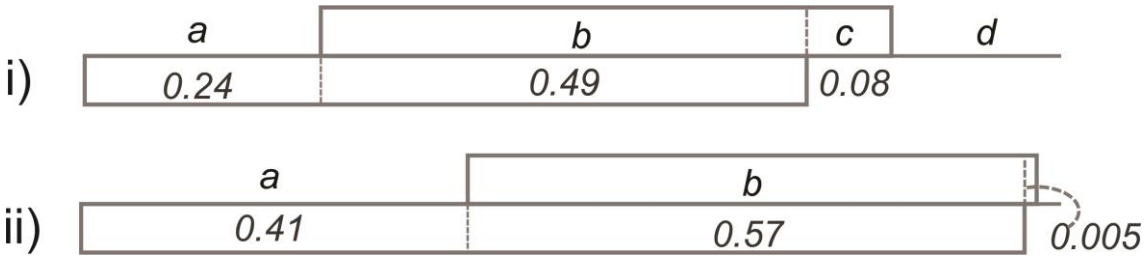

Fig. 4. Partial coefficients of determination (R^2) for (i) richness of new mammal species and (ii) richness of old mammal species. Component *a* represents the exclusive fraction of the environmental variables (temperature, AET, TxRelev and NDVI), component *b* represents the shared explanation between environmental variables and spatial filters, component *c* is the contribution of unaccounted variable that are spatially structured and component *d* illustrates the variance unexplained by the models.

4 DISCUSSION

Niche conservatism has been highlighted as an important mechanism for understanding biological processes and patterns (Webb et al. 2002; Wiens & Graham 2005; Losos 2008). The tropical niche conservatism hypothesis proposes how niche conservatism over evolutionary time might have shaped global current species distributions (Wiens & Donoghue 2004; Wiens 2007, Hawkins, Diniz-Filho, & Soeller 2005, Hawkins et al. 2006). Under this mechanism, it is expected that species conserve the ecological characteristics present in evolutionary times that they originated. Studies evaluating species ecological niche attributes of clades with distinct geographical and/or climatic histories, have shown that species of basal clades are generally restricted to warm and wet conditions, while species of more derived clades are richer in colder and drier habitats (e.g. Hawkins, Diniz-Filho, & Soeller 2005; Hawkins et al. 2006, 2007; Hawkins & DeVries 2009; Wiens et al. 2006; Buckley et al. 2010, Romdal et al. 2013).

In this study, we found that the differences in ecological correlates of old and new mammal species are highly dependent on the taxonomic scale. Results of analysis including all clades show that recent and old species have similar response to current environmental conditions. However, when we investigated the climate-richness relationships at higher taxonomic scales, distinct patterns emerged. Although evapotranspiration was the strongest predictor of species richness for most of the studied clades (i.e. higher richness in warmer and wetter places), we found discrepancies in the direct effects of temperature and/or vegetation on richness patterns among clades. Another

important issue addressing the global pattern of mammal species richness is the presence of spatial structure in the data, with major portions of variance being explained by regional spatial structure of environment. The components that accounted for the effect of omitted spatially structured variables and the unexplained variation were very low, indicating that our model included the most important environmental variables and explained most of the variation in mammal species richness. It is important to note that, when combining all clades, the similarity between ecological correlates of old and new species is disproportionally affected by the climate-richness relationship of bats, which is the richest order in our study.

The analyses for bats suggest that, regardless of the species ages (i.e. in which ecological conditions they originated), bats will have similar environmental correlates (new and old bat species occupying similar environmets). While some studies have suggested niche conservatism as a main driver of geographical patterns in bats (Stevens 2011; Villalobos, Rangel, & Diniz-Filho 2013), other find weak or no support for the hypothesis (Dormann et al. 2010; Pio 2010; Ramos Pereira & Palmeirim 2013; Arita, Vargas-Barón & Villalobos 2014, Villalobos et al. 2014). In our study we also found no evidence for the tropical niche conservatism in bats. Pio (2010) suggested some ecological characteristics that could have led to lack of phylogenetic structuring in climatic niche of bats. They argued that as bats are good at resource partitioning and present exceptionally high diversity in very restricted areas (Kalko 1998), hence, the pressure to occupy different macro climatic niches and to separate distributional ranges may not be very strong. Apart from that, their dispersal and migratory capacities (Hedenstrom 2009; Corlett 2009) may allow them to overcome local harsh climate conditions. Therefore, constraints on occupancy of climatic niche may be attenuated by other limiting factors that play a more significant role for bats.

On the other hand, our results for carnivores may lead to alternative conclusions. Old species of the order Carnivora are richer in warmer environments, whereas new species show negative climate-richness path coefficients. Investigations of the geographical distributions of species ages complement these findings, showing that new species of Carnivora are adapted to cooler climates and are richer across the temperate zones and in mountains

in the tropics, whereas old species are confined to warmer tropical regions (Pie et al. *in prep.*). Current climatic correlates for carnivores might reflect the environmental conditions extant in evolutionary times in which they were generated, being consistent with niche conservatism hypothesis and in concordance with previous findings for birds (Hawkins et al. 2006) and mammals (Buckley et al. 2010),

Marsupialia also presented differences in the ecological correlates of old and new species, with higher diversity of new species in communities of lower availability of water and energy. In contrast to eutherian orders, marsupials have a rather unusual geographic distribution, with three orders restricted to the Americas and four orders inhabiting only Australasia (Nilsson et al. 2004; Springer, Krajewski, and Meredith 2009). Furthermore, species richness gradients of Marsupialia are largely driven by new species in the Australian region, whereas the Americas are dominated by old species (Pie et al. *in prep*). We propose that global differences in the ecological correlates for new and old species might be primarily explained by the marsupial biogeographical history. New species of Marsupialia, which are richer in Australasia, presented a negative path coefficient for AET, whereas old Neotropical species had a positive AET-richness relationship. Likely, this is given the differences between the tropical forests and Australian xeric habitats. When the analyses are run for both continents together, Australia is compressed into a small portion of the AET gradient, and given Australia is dominated by new species, the coefficient for these species became negative.

We found influences of distinct ecological predictors in marsupial richness in Australasia and the New World. In the Australian continent, both old and new species had positive AET and negative temperature coefficients. As the greatest part of the continent is desert or semi-arid, species richness peak in regions of moderate climates (temperate, tropical and subtropical regions), leading to the negative temperature coefficient found in both, old and new species. Old species are essentially richer in regions with higher plant productivity, but NDVI was not an important predictor of marsupial new species. Australia has not always been arid, but has undergone changes in climate and vegetation cover over the evolutionary time (Martin 2006, Behresmeyer et al. 1992). At the beginning of the Cenozoic, continental Australia was mainly

covered by meso-micro-thermal rainforests. The early-mid-Miocene was warm-humid and there was a considerable diversity of forest types. In the late Miocene, Australia became cooler and drier, with a major reduction of rainforests and an increase of aridity and open dry forests, grasslands and deserts. Rainforests continued to decrease during the Pliocene and by the early Pleistocene, the modern arid climatic regime had already been established (Martin 2006, Behresmeyer et al. 1992). Origin of old marsupial species dates to the epoch when Australia was warm-humid with considerable diversity of forest types. Our results might indicate that old species which could not cope with these changing in vegetation cover, remained mainly in more densely vegetated regions. For Neotropical marsupials, instead of vegetation, opposite effects of the ecological correlates for old and new species are evidenced in availability of water and energy. Arid Neotropical regions are dominated by new species, whereas old species are richer in wetter and warmer climates. Our findings for marsupials indicate that, besides the variation within clades, there is also variation in the ecological niche components of new and old species within distinct biogeographical regions.

Artiodactyls and primates results contradicted our expectations. Artiodactyls have more representatives of old species in communities where plant productivity is lower and primates contradicted the expectations in relation to temperature, with peaks of old species richness in cooler climates. Disagreement regarding whether climatic niches are conserved in mammal has already been evidenced in the literature (Dormann et al. 2010; Kamilar & Muldoon 2010; Arita, Vargas-Barón & Villalobos 2014). It has also been shown that the degree of niche conservatism in mammals varies among groups in relation to their characteristics (tropical x temperate, small-ranged x large-ranged, generalist x specialist; Cooper et al. 2011).

In our study, we found that richness patterns of old and new mammal species are driven by distinguish ecological correlates. However, we did not found any pattern repeated among species but the ecological correlates of species richness patterns can be influenced by clade identity and species ages. Our investigation of species richness–climate relationship utilizing direct inferences of species ages does not hold consistently with the predictions of TNC, as opposed to studies with higher taxonomic groups (Buckley et al. 2010,

Romdal et al. 2013). The statistical signal of tropical niche conservatism should be stronger for lower-level clades because the conservatism of the climatic niche should decrease through time (Wiens & Donoghue, 2004). Contrary to this expectation, our species-level analysis found inconsistent evidence for tropical niche conservatism. Therefore, idiosyncrasies of clades are important and care must be taken when making general predictions from results obtained from restricted taxonomic scales. Our study challenges the traditional view that niche conservatism is the main driver underlying the ubiquitous climate-richness pattern.

6 REFERENCES

Aplin, K.P. & Archer, M. (1987) Recent advances in marsupial systematics with a new syncretic classification. *Possums and opossums: studies in evolution.* (ed. Archer M) Sydney: Surrey Beatty and the Royal Zoological Society of New South Wales, 15–72.

Arita, H., Vargas-Barón, J. & Villalobos, F. (2014) Latitudinal gradients of genus richness and endemism and the diversification of New World bats. Ecography, **37**, 1024–1033.

Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H. & Wing, S.L. (1992) Terrestrial Ecosystems Through Time. Evolutionary Paleoecology of Terrestrial Plants and Animals, University of Chicago Press, Chicago, USA.

Bininda-Emonds, O., Cardillo, M., Jones, K., MacPhee, R., Beck, R., Grenyer, R., Price, S., Vos, R., Gittleman, J. & Purvis, A. (2007) The delayed rise of present-day mammals. Nature, **446**, 507–12.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. Ecology **73**,1045-1055.

Brown, J.H. (2014) Why are there so many species in the tropics? Journal of Biogeography, **41**, 8–22.

Buckley, L., Davies, T., Ackerly, D., Kraft, N., Harrison, S., Anacker, B., Cornell, H., Damschen, E., Grytnes, J.-A., Hawkins, B., McCain, C., Stephens, P. & Wiens, J. (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2131–8.

Chown, S.L. & Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. Trends in Ecology & Evolution, **15**, 311–315.

Conway, G. (2007) A Doubly Green Revolution: ecology and production. Theoretical Ecology: Principles and Applications, 3rd edn (eds R, May & A, McLean), pp.158-171. Oxford University Press, Oxford

Corlett, R. T. (2009) Seed Dispersal Distances and Plant Migration Potential in Tropical East Asia. *Biotropica,* **41,** 592-598.

Currie, D., Mittelbach, G., Cornell, H., Field, R., Guégan, J., Hawkins, B., Kaufman, D., Kerr, J., Oberdorff, T., O'Brien, E. & Turner, J. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters, **297**, 1548–51.

Dormann, C.F., Gruber, B., Winter, M., & Herrmann, D. (2010) Evolution of climatic niches in European mammals. Biology Letters, **11**, 229-232.

ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Field, R., Hawkins, B., Cornell, H., Currie, D., Diniz-Filho, J., Guégan, J., Kaufman, D., Kerr, J., Mittelbach, G., Oberdorff, T., O'Brien, E. & Turner, J. (2009) Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography, 36, 132–147

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. The American Naturalist, **161**, 523– 536.

Fox, J., Kramer, A. & Friendly, M. (2013) SEM: structural equation models. R package version 3.1-3.

Gaston, K. (2000) Global patterns in biodiversity. Nature, **405**, 220–7.

Gaston, K. & Blackburn, T. (1996) The Tropics as a Museum of Biological Diversity: An Analysis of the New World Avifauna. Proceedings of the Royal Society B: Biological Sciences, **263.**

Gouveia, S.F., Villalobos, F., Dobrovolski, R., Beltrão-Mendes, R. & Ferrari, S.F. (2014) Forest structure drives global diversity of primates. The Journal of animal ecology.

Griffith, D.A. & Peres-Neto, P.R. (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. Ecology, **87**, 2603–2613.

Hawkins, B.A., R. Field, H.V. Cornell, D.J. Currie, J-F. Guégan, D.M. Kaufman, J.T. Kerr, G.G. Mittelbach, T. Oberdorff, E.M. O'Brien, E.E. Porter & J.R.G. Turner (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology **84**: 3105-3117

Hawkins, B.A, Diniz-Filho, J.A & Soeller, S.A (2005) Water links the historical and contemporary components of the Australian bird diversity gradient. Journal of Biogeography, **32**.

Hawkins, B.A., Diniz-Filho, J.A., Jaramillo, C.A. & Soeller, S.A (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. Journal of Biogeography, **33**.

Hawkins, B.A., Diniz-Filho, J.A., Jaramillo, C.A. & Soeller, S.A. (2007) Climate, niche conservatism, and the global bird diversity gradient. *The American naturalist*, **170**, S16–27.

Hawkins, B.A. & DeVries, P. (2009) Tropical niche conservatism and the species richness gradient of North American butterflies. Journal of Biogeography, **36**, 1698–1711.

Hawkins, B.A, McCain, C., Davies, T., Buckley, L., Anacker, B., Cornell, H., Damschen, E., Grytnes, J., Harrison, S., Holt, R., Kraft, N. & Stephens, P. (2012) Different evolutionary histories underlie congruent species richness gradients of birds and mammals. Journal of Biogeography, **39**, 825–841.

Hedenstrom, A. (2009) Optimal migration strategies in bats. *Journal of Mammalogy,* **90,** 1298-1309.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones P.G., & Jarvis, A (2005) Very high resolution interpolated climate surfaces for global land areas. .

IUCN. (2010) Red List of threatened species published at http://www. iucnredlist.org.

Jablonski, D., Roy, K. & Valentine, J. (2006) Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity Gradient. Science, **314**, 102–6.

Kalko, E.K.V. (1998) Organisation and diversity of tropical bat communities through space and time. Zoology-Analysis of Complex Systems, **101**, 281-297.

Kamilar, J.M. & Muldoon K.M. (2010) The Climatic Niche Diversity of Malagasy Primates: A Phylogenetic Perspective. PLoS ONE 5(6): e11073. doi: 10.1371/journal.pone.0011073

Knipling, E. B. (1970) Physical and physiological basis for the reflectance of visible and near-20 infrared radiation from vegetation. Remote Sensing of Environment. **1**,155-159

Latham, E.L. & Ricklefs, R.E. (1993) Continental comparisons of temperate-zone tree species diversity. Species diversity in ecological communities:

historical and geographical perspectives (eds R.E. Ricklefs and D. Schluter), pp. 294–314. University of Chicago Press, Chicago.

Lewin, R. (1989) Biologists disagree over bold signature of nature. Science **244**, 527-528.

Liu, Y.J., Arens, N., & Li, C.S. (2007) Range change in *Metasequoia*: relationship to palaeoclimate. Botanical Journal of the Linnean Society, **154**, 115–127.

Losos, J. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters, **11**, 995–1003.

Martin, H.A. Cenozoic climatic change and the development of the arid vegetation in Australia. Journal of Arid Environments, **66**, 533-563.

Mittelbach, G., Schemske, D., Cornell, H., Allen, A., Brown, J., Bush, M., Harrison, S., Hurlbert, A., Knowlton, N., Lessios, H., McCain, C., McCune, A., McDade, L., McPeek, M., Near, T., Price, T., Ricklefs, R., Roy, K., Sax, D., Schluter, D., Sobel, J. & Turelli, M. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology letters*, **10**, 315–31

Nilsson, M., Arnason, U., Spencer, P. & Janke, A. (2004) Marsupial relationships and a timeline for marsupial radiation in South Gondwana. Gene, **340**, 189196.

Nyakatura, K. & Bininda-Emonds, O. (2012) Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. BMC Biology, **10**, 12.

Pearman, P., Guisan, A., Broennimann, O. & Randin, C. (2008) Niche dynamics in space and time. Trends in Ecology & Evolution, **23**, 149–58

Pereira, M. & Palmeirim, J. (2013) Latitudinal Diversity Gradients in New World Bats: Are They a Consequence of Niche Conservatism? *PLoS ONE*, **8**, e69245.

Pio, D. (2010). No macro-climatic niche conservatism in southern African bats. PhD thesis, Université de Lausanne, Lausanne.

R Development Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahbek, C. & Graves, G. (2001) Multiscale assessment of patterns of avian species richness.*Proceedings of the National Academy of Sciences*, **98**, 4534–9.

Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for spatial analysis in macroecology. Ecography, **33**,46–50.

Rettallack, G. J. (2001) Cenozoic Expansion of Grasslands and Climatic Cooling The Journal of Geology, **109**, 407–426.

Ricklefs, R. (2004) A comprehensive framework for global patterns in biodiversity. Ecology Letters, **7**.

Rolland, J., Condamine, F., Jiguet, F. & Morlon, H. (2014) Faster Speciation and Reduced Extinction in the Tropics Contribute to the Mammalian Latitudinal Diversity Gradient. *PLoS Biology*, **12**, e1001775.

Romdal, T., Araújo, M. & Rahbek, C. (2013) Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecology and Biogeography*, **22**.

Rosenzweig, M.L. (1968) Net Primary Productivity of Terrestrial Communities: Prediction from Climatological Data. The American Naturalist, **120**, 67–74.

Rouse, J.W. (1974) Monitoring the vernal advancement of retrogradation of natural vegetation. NASA/GSFC, Type III,Final Report, Greenbelt, MD, pp. 371.

Shipley, B. (1997) Cause and correlation in biology. The American Naturalist **149**, 1113-1138.

Springer, M.S., Krajewski, C.W. & Meredith, R.W. (2009) Marsupials (Metatheria). *The Timetree of Life*, Pp. 446-470 (eds.S. B, Hedges & S, Kumar) Oxford University Press

Stein, A., Gerstner, K., Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters, pp. 866–880.

Stephenson, N.L. (1990) Climatic control of vegetation distribution - the role of the water balance. The American Naturalist, **135**, 649-670.

Villalobos, F., Rangel, T. & Diniz-Filho, J. (2013) Phylogenetic fields of species: cross-species patterns of phylogenetic structure and geographical coexistence. Proceedings. Biological sciences / The Royal Society, 280, 20122570.

Villalobos, F., Lira-Noriega, A., Soberón, J. & Arita, H. (2014) Co-diversity and co-distribution in phyllostomid bats: Evaluating the relative roles of climate and niche conservatism. Basic and Applied Ecology, 15, 8591.

Webb, C., Ackerly, D., McPeek, M. & Donoghue, M. (2002) PHYLOGENIES AND COMMUNITY ECOLOGY. Ecology and Systematics, **33**.

Wiens, J. & Donoghue, M. (2004) Historical biogeography, ecology and species richness. Trends in Ecology & Evolution, **19**, 639–44.

Wiens, J. & Graham, C. (2005) NICHE CONSERVATISM: Integrating Evolution, Ecology, and Conservation Biology. Annual Review of Ecology, Evolution, and Systematics, 36

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. The American naturalist, **168**, 579–96.

Wiens, J.J. (2007) Global patterns of diversification and species richness in amphibians. The American Naturalist, **170**, S86–S106.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.-A.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M. & Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecology letters, **13**, 1310–24.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) LATITUDINALGRADIENTS OFBIODIVERSITY: Pattern, Process, Scale, and Synthesis. Ecology, Evolution, and Systematics, 34.

Willmott, C.J. & Matsuura, K. (2001): Terrestrial Water Budget Data Archive: Monthly Time Series (1950-1999).

Wilson, D.E. & Reeder D.M. (1993) Mammal species of the world: a taxonomic and geographic reference. Baltimore (MD): The Johns Hopkins University Press.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. Science, **292**, 686–93